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I.—On the Structure of the Diatomaceous Frustule, and its Genetic Cycle. By John Denis Macdonald, M.D., F.R.S., Staff-Surgeon, R.N.

[Plate III.]

From close examination of some of the larger forms of Diatomaceæ, more especially species of *Isthmia* and *Biddulphia*, I have long been under the impression that the commonly received views of the structure of the frustule and its mode of self-division require considerable modification. Though numerous inquirers have been engaged in the very inviting study afforded by these little organisms, I am not aware that any one has yet traced out their genetic cycle as satisfactorily as could be wished.

Having consulted the works of various authorities upon this subject, I find the views expressed in the writings of Dr. Wallich (particularly in his paper on *Triceratium*, vol. vi. Journal of Microscopical Science, p. 242, and on the Diatomvalve, vol. viii. Trans. Micr. Sci. p. 129) most in accordance with my own independent researches.

Dr. Wallich appears to have been the first to set forth clearly that the middle piece or "zone" consists, while the frustule is intact, of two distinct plates, the one received within the other, and that the growth of such plates can only take place at the free margins, or those which are not connected with the valves.

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He has also shown how the capacity of the frustule may be augmented, at least in one direction, by the sliding out of those plates or "rings" telescope-fashion to accommodate themselves to the increase of the contents during division. This great fact is barely shadowed forth in Griffith and Henfrey's 'Micrographie Dictionary' (ed. 1856), p. 201, where it is said that "in Biddulphia and Isthmia, and similar forms, the new half-frustules formed inside the 'hoop' slip out from it like the inner tubes from the outer case of a telescope." The "inner tubes" in this case would of course be the hoops of the new valves, which in their turn assist in forming a so-called "intermediate piece" with their parent valves, though this is not specifically stated, and, strangely enough, a different inference may be drawn from the following quotation (op. cit. p. 199): the frustules of Diatomaceæ are described as consisting of "two usually symmetrical portions or valves comparable to those of a bivalve shell, but are in contact at their margins with an intermediate piece (the 'hoop'), variable in breadth, according to age." This view of the structure of the frustule is substantially the same as that given by Smith in his introduction to the 'Synopsis of the British Diatomacee,' only that he makes the hypothetical intermediate piece or "hoop" more insignificant by calling it a "connecting membrane," whereas it is in reality double, as before stated, one portion being included within the other, so as to admit of extension of the frustule in the direction of the axis of growth.

Each of these sliding segments, moreover, is not merely connected but directly continuous with the body of its own valve, that which is invaginated being always the younger, having been produced within the other or the parent valve by an endogenous process, combining fission with growth and remodelling of the primordial utricle. Whatever be the configuration of the true ends of the frustule, or, in other words, the body of the valves, viz. circular, triangular, foursquare, or navicular, the sides or "hoops" of the two forming the so-called "intermediate piece" are, as it were, marginal extensions of them, but perpendicular to their general plane. Quoting, again, from the 'Micrographic Dictionary,' p. 200, it is stated that "the ordinary mode of increase of the cells of Diatomaceæ is, like that of other vegetable cells, a process of division. . . . It may be briefly described thus:—the primordial utricle, enclosing the contents, divided into two portions, which separate from one another in a plane parallel with the sides of the individual frustules; the two valves of the parent cell gradually separate from one another, remaining connected by the simultaneous gradual widening of the

'hoop.'" This description would lead one to suppose that the hoop was a single and distinct segment, serving to connect those portions of the frustule to which the term valves is more particularly confined, and that the growth of the hoop was, therefore, not limited to one border more than the other.

Dr. Wallich, I think, very successfully refutes the idea of a continuous growth of the Diatomaceous frustule, the fact being, as he states, that "the variation in the size of the valve and the number of its strice proceed pari passu during the process of division, but not subsequently." He admits that "growth may take place to the extent of new siliceous matter being secreted along the margins of the valve, its depth being thereby augmented;" but he considers it highly probable "that the connecting zone by which the young valve is protected during its secretion and consolidation determines the limit of the dimensions to be attained by it." He states, moreover, that "in truth no two valves of the same frustule can be of the same size, for the new valves, being formed within the 'connecting zones' of the parent frustule, must be smaller than these." This, I should think, is the essential cause of the great diversity of size observable in frustules of the same species being constant and universal; but he lays more stress upon the peculiar idiosyncrasy of the sporangial frustule, vicissitudes of climate, and increased or diminished sources of nutritive matter. Notwithstanding all the above important facts and deductions, in common with other authors Dr. Wallich seems to consider the hoops of the "connecting zone" quite supplementary, and not essentially persistent parts of the valves themselves, though often easily separable.

In the 'Micrographic Dictionary,' at p. 201, we read, "The hoop appears to be a provision for the protection of the nascent half-frustnles, which probably do not become silicified until full-grown, and would thus be liable to be injured or disturbed by the movements of the rigid and heavy parent half-frustules if the centre of the frustule in process of division was naked, as in the Desmidiaceae." In all this the existence of two distinct layers in the "hoop" is not even hinted at, nor their identity each with its own valve at the true ends of the

frustule.

It stands to reason that as the two new half-frustules are developed endogenously, or within their parents, the former must be smaller than the latter by the whole thickness of the siliceous investment; and this will continue to be the case gradatim in the direct line of descent, though of course all the pullulations successively taking place in the same half-frustule will be uniformly of the same size, holding the relation of cast

to mould with respect to their developing cell. Seeing, therefore, that the smaller the frustules of the same species are the more endogenous developments must have preceded them, and therefore, as one would naturally suppose, the nearer must be the fitness for conjugation to complete the genetic cycle, my great difficulty at one time was to know how the frustules of a given species ever regained their original size, or where this gradual diminution should end; but Mr. Thwaites has furnished us with the solution in his important discovery that the sporangial frustule resulting from the process of conjugation is so much larger than the parent cells. In relation to this subject we read (op. cit.):—"A great difficulty meets us here. The necessary consequence of the conjugation just described is, that every species in which it occurs must be represented by two forms, one small and the other large, between which a gap exists, over which we have at present no means of bridging, except by supposing that the two new halves formed in cell-division need not always be equal, and that by dwindling away through a succession of steps of this kind the progeny of the sporangial frustules may be reduced to the original size." This may be very ingeniously conceived; but the true key to the difficulty does not appear to have been apprehended by the writer. Mr. Smith, moreover, widens the breach by assuming a diametrically opposite hypothesis, in which, however, he only seems to account for difference of size, without observing the dilemma into which he falls. Thus he says at p. xxvi of his work, already alluded to, speaking of self-division, that "a careful examination of the process in the filamentous species has led him to conelude that a slight enlargement occasionally takes place in the new valves, thus causing a widening of the filament;" and reasoning upon this premiss, which, I humbly conceive, should have been taken the other way, he proceeds as follows:--"The increase in the new valves, although slight, will, however, sufficiently account for the varying breadth of the bands of the filamentous species, and the diversity of size in the frustules of the free forms, without obliging us to suppose that a growth or aggregation takes place in the siliceous valve when once formed." Yet it is actually within the fully formed valve that the new half-frustule is produced; and if so, it must, as before stated, be smaller than its parent by the whole thickness of the siliceous coat. "Starting from a single frustule," he goes on to say, "it will be at once apparent that if its valves remain unaltered in size while the cell-membrane experiences repeated self-division, we shall have two frustules constantly retaining their original dimensions, four slightly increased,

eight somewhat larger, and so on in a geometrical ratio, which will soon present us with an innumerable multitude containing individuals in every stage, but in which the larger sizes predominate over the smaller; and such are the circumstances ordinarily found to attend the presence of large numbers of these organisms." I am afraid that this doctrine of a geometrical increase in the size of the frustules will not stand the test either of fair theoretical induction or comparison with natural fact; for although there is in truth a gradual diminution, even this does not take place in a geometrical ratio, which, in the nature of the case, can only apply to number, not to size, as will be clearly seen on inspecting fig. 5, purporting to trace the history of a single frustule through five grades of self-division, in which the numbers accurately express the relative sizes of all the half-frustules, new and old.

It is now full time to elucidate my own views by illustrative facts, which I hope will be considered satisfactory, as supporting all the observations previously made, and by inference affording a guide to the study of those forms which, from their extreme delicacy and minuteness, might be for ever problematical and difficult of analysis, both as to structure and

physiology.

As each perfect frustule consists of an older and a younger valve, never of two valves of the same age, Kützing's names, primary as applied to the former, and secondary to designate the latter or the invaginated valve, can be open to no possible objection. But to these it is absolutely necessary to add two tertiary valves of the same age, resulting from the process of fission, viz. the first tertiary, developed in connexion with the primary valve, and the second tertiary, forming a new frustule with the secondary valve.

Of all these valves the primary or most external is the largest, the secondary and first tertiary are intermediate, while

the second tertiary is the smallest.

Fig. 1 (Pl. III.) is a diagrammatic section of a perfect frustule previously to the transverse fission of its primordial utricle and contents.

a. Primary valve.a 1. Body of the valve.a 2. Primary hoop.

b. Secondary or invaginated valve.b 1. Body of the valve.

b 2. Secondary hoop.

Fig. 2 represents a perfect frustule after the fission of the primordial utricle and contents and the formation of c and d, the first and second tertiary valves of the same age, and consisting of c 1 and d 1, the body of the valves, and c 2 and d 2, the incipient tertiary hoops. The remaining references are the same as in fig. 1.

Fig. 3 illustrates the ultimate separation of the two new frustules, in which the same process is repeated: A, the primary-valve frustule; B, that of the secondary valve. The smaller letters and numbers correspond with those in the foregoing figures.

In fig. 4, 1, 2, and 3 are ordinary examples of *Biddulphia*, drawn from nature for comparison with figs. 1, 2, 3 respec-

tively, which are diagrammatic.

On submitting a large frustule of *Isthmia* to microscopic examination, the pitting or markings of the invaginated hoop may be distinctly focussed through the enclosing or external one connected with the primary valve; and it is remarkable that the artists employed by various writers to illustrate their works have shown this unequivocally in many instances, militating irreconcilably with the text.

The "hoops" of the tertiary valves are gradually evolved as the new frustules progress in development; and even while included within their formative valves their markings are often

elearly discernible.

Before the tertiary "hoop" is of sufficient depth to give the new frustule its adult dimensions, the outer "hoop" will be seen to extend beyond the gibbous fulness of the younger valve in *Biddulphia* and *Isthmia*—a condition which is incompatible with the idea of a single "intermediate piece" or "connecting membrane" of the existing theory. Any deepening of the so-called connecting membrane is therefore only likely to happen in connexion with the tertiary hoop, no addition being necessary, nor, indeed, at all capable of proof, as respects the adult or outer "hoop." Dr. Wallich, however, assumes that additions are made to both in the manner above alluded to.

Of course, in particular genera, where the hoops of the valves are exquisitely thin and destitute of markings, it would be more difficult to trace out the particulars just described. The inference, however, appears legitimate, unless sufficient reasons can be advanced to warrant a contrary opinion, that, small and large, the same general laws of development obtain with all the Diatomaceæ. To conclude these remarks, it must be stated that every tertiary valve becomes in due course secondary, and ultimately primary, beyond which there is no further advance; but after having been the parent of an almost unlimited progeny it must tend to decay, if it be not privileged to close a genetic cycle by taking part in the development of a sporangial frustule from which another living chain may descend with renewed energy.

Mr. Ralfs uses the term "front view" for what appears to

me to be in reality the "side view" of the frustule, corresponding with the position in which the axis of growth is perpendicular to the axis of vision, or, in other words, where the component frustules would form a band or filament seen sideways. On the other hand, when such a filament is seen end on, the axis of growth being coincident with the axis of vision, he would call the presenting end of the nearest frustule a "side view," though this is unquestionably an end view by all analogy.

It appears to me that the axis of growth should be the longitudinal axis, however short that may be, though the broadest diameter is generally recognized as the length of the

frustule.

Besides the siliceous envelope and the amber tint of the contents, the Diatomaceæ differ very materially from the Desmidiaceæ in their process of self-division. Thus, in the latter, more especially the solitary species, fission is attended with the immediate and total separation of the valves, followed by genuine gemmation of a new valve from each parent. In the Diatomaceæ, on the contrary, fission takes place under cover of the sliding hoops, which retain the original valves in contact, while the new endogenously developed half-frustules are rather being modelled out of the preexisting material than

produced by genuine gemmation as in Desmidiaceæ.

In the annexed diagram (fig. 5) I have attempted to trace the history of a single Diatomaceous frustule through several stages of self-division, expressing by simple figures the relative sizes of all the half-frustules. As a guide to the method adopted, it will only be necessary to bear in mind that valve No. 1 is the parent of valve No. 2, valve No. 2 the parent of valve No. 3, &c., the rising numbers representing the grades of diminution—which are certainly not in a geometrical ratio, like the simple multiplication of the frustules themselves. It will be seen that all the frustules to the left of the median line are the progeny of the primary valve, and those to the right the descendants of the secondary valve; and taking the grades in their order, we find, on the primary side, 1 in the first place, 2 in the second, 3 in the third, 4 in the sixth, 5 in the eleventh, and 6, the highest number, in the twenty-second. The highest numbers are also to be found in corresponding places on the secondary side, and the ratio is certainly much more complex than the geometrical.

Fig. 6 shows an undulating line by construction, giving each valve of the long series its relative breadth within seven thicknesses of the siliceous coat, but only representing one border; the progeny of valve 7 must exhibit a very ap-

preciable diminution in size as compared with the original sporangial frustule; and in this theory every requisite for the completion of the genetic cycle of the species would appear to be supplied.

II.—On Physalia and certain Scombroid (?) Fish which are frequently associated with it in Tropical and Subtropical Seas. By G. C. Wallich, M.D., F.L.S.

Mr. Collingwood's interesting paper on "Oceanic forms of Hydrozoa," which appeared in the 'Annals' for November 1867, brought to my recollection some additional facts in connexion with *Physalia* which came under my observation during repeated voyages to and from India, and of which I retain copious notes. To these facts I will advert immediately; but I would point out, en passant, that the stinging-properties of this Hydrozoon are by no means so novel as Mr. Collingwood seems to think, every sailor with whom I have come in contact who has once traversed tropical and subtropical latitudes having been well aware that the "Portuguese man-of-war" is not a creature to be handled with impunity. The stinging-property resides in the tentacles, not in the polypites, and is produced by the discharge of acontia from minute oval sacs which are distributed at regular intervals along these organs.

Although I have invariably failed in my efforts to preserve the pneumatophore of *Physalia* in anything approaching to its pristine condition, I have been able readily to secure the tentacles in such a manner as to have retained their character up to the present period, namely, over a space of eleven years. This has been effected simply by placing the pneumatophore on a card or board (to which it adheres at once through a certain tenacity peculiar to it) and by then winding off the tentacle in the same way that one may wind off a skein of silk or cotton. The extensile quality of the organ is such that I have sometimes succeeded in stretching it, from its natural length of from 3 to 6 inches, to some 8 or 10 yards, and this without once breaking the continuity of the thread. On being so extended, the tentacle forms an extremely delicate flattened band, composed of several parallel fibres of highly contractile tissue arranged longitudinally, each fibre being from \(\frac{1}{2500}\) to \(\frac{1}{1700}\) of an inch in diameter*. On this, or, rather, imbedded in this composite filament, the acontiasacs are distributed.

^{*} A specimen of a piece of the preserved tentacle, mounted on an ordinary slide in Canada balsam, without further preparation, is to be seen in the cabinet presented by me to the Royal Microscopical Society.